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Dear Abnormal and the like
Gentlemen and女士们 of the
British and American
Parliamentary Association.
My dear Mr. Justice.
Sir. etc. etc. etc. etc.

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
AGRICULTURAL SCIENCES

Vol. 3, No. 3, pp. 37-54, plate 12

September 29, 1917

SOME ABNORMAL WATER RELATIONS IN
CITRUS TREES OF THE ARID SOUTH-
WEST AND THEIR POSSIBLE
SIGNIFICANCE

BY
ROBERT W. HODGSON

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INTRODUCTION

The progress of the development of the citrus industry, in general, and that of California in particular, has frequently been retarded or temporarily stopped by serious obstacles in the form of insect pests or plant diseases. Some of the most baffling of these troubles fall naturally into a group which for want of a better name has come to be known as that of "physiological diseases," which are thought to be caused by various obscure derangements of nutrition or other vital functions. This group includes mottled-leaf, die-back, chlorosis, June drop, puffing of the fruit, and others of less importance. Knowledge of the true nature of this class of diseases is extremely meager in spite of the fact that they have received much earnest attention from scientific investigators; and little can be accomplished in the way of devising control measures until much more is known in regard to them. Nor can we hope to progress far beyond the realm of speculation without greatly augmenting our knowledge of the physiology and anatomy of the normal citrus tree when grown under any one of a series of very widely varying environmental complexes which obtain in different parts of the arid southwest.

It is, therefore, proposed to attempt by means of a series of systematic experimental studies to obtain some definite and accurate information on the physiology of the genus *Citrus*. It is hoped that the results may serve as a basis for the elucidation of some, at least,

of the important problems referred to above. The studies in question will attempt to shed light on transpiration problems, nutrition problems, and others equally important. The paper which is submitted herewith forms an introductory contribution to the subject under investigation.

The writer is not unaware of the essential similarity between the physiological problems presented by citrus and other fruit trees. He has chosen, however, to study the physiology of the citrus tree as a separate entity because of the reasons given above, and the further one that the peculiar climatic conditions under which this tree is frequently placed in the arid southwest, demand a special treatment. Doubtless much may be gained from these studies which will apply to physiological problems connected with other trees.

The data here presented were obtained during an investigation of one of the so-called physiological diseases above mentioned, namely, the June drop.¹ Ever since the Washington Navel orange has been grown in the dry interior valleys of Arizona and California, this variety has been subject to excessive dropping of the young fruits. This has come to be known popularly as the June drop although the fall of the fruits is by no means confined to June but may occur at any time from petal fall, in April, until the fruit reaches several inches in diameter in August. The prevalence and amount of this dropping seems to be influenced to a marked degree by certain environmental factors to which the trees are subject. The regular annual shedding of the young fruits is most serious in regions where the annual precipitation is lowest, the mean summer temperature highest, atmospheric humidity lowest, solar radiation most intense, and air movement greatest during the growing season. That the excessive drop of young fruit is in some way intimately connected with extreme climatic conditions is indicated by the fact that in some parts of southern California, where the drop is ordinarily not excessive, the hot wave of June 15-17, 1917, during which a temperature of 118° F was experienced in the Riverside and Redlands districts, was immediately followed by a drop so severe that practically the entire young crop of navel oranges was lost.

The experimental work from which the data were obtained was carried on at Edison, Kern County, California. Edison comprises

¹ This investigation, which is now in progress, was carried on in collaboration with Professor J. Eliot Coit who planned the first series of experiments and began the work in February, 1916. A joint-authorship paper correlating this and other aspects of the June drop phenomenon is in course of preparation.

a small colony of about seven hundred acres of orange orchard located eight miles southeast of Bakersfield and surrounded on two sides by typical desert of the southern San Joaquin valley, with its characteristic semixerophytic flora. Extreme climatic conditions, as above mentioned, are operative there but the Washington Navel orange matures early and is of excellent quality, although crops are small because the drop referred to is excessive.

WATER RELATIONS AND ABSCISSION

It has long been recognized that abnormalities or irregularities in the water relations of plants are often associated with the abscission of various plant parts. Balls² was able to cause complete shedding of leaves, flower buds, and bolls of the cotton plant *Gossypium herbaceum* within four days by pruning the roots and so limiting the ability of the plant to take up water. Lloyd³ in his investigation of the cause of abscission in the same plant came to the conclusion that the causative factor lay in a steady decrease in the moisture content of the soil in contact with the roots of the plant. This reduction causes a severe tax on the power of the plant to maintain normal water relations and results in fluctuations in the water content of the aerial parts which, in turn, leads to abscission.

Although the work of Lloyd was performed in the humid southern states, he makes the statement that "there seldom occurs a day on which there is no minus water fluctuation in the plant." He based this conclusion not only on data derived from shedding records but also on a study of transpiration rates, and water deficit in the leaves. In connection with his observations on the effect of temperature in causing acceleration of abscission, he came to the conclusion that "the water deficit is the cause of the rise of temperature in the tissues and that this constitutes the stimulus which directly leads to abscission."

Other evidence of the occurrence of marked deficits in the water content of plant organs is not lacking. Livingston and Brown,⁴ working with a number of plants growing near Tucson, Arizona, found that (with the exception of the true xerophytes as *Covillea* and *Prosopis*) during the afternoon the leaves suffered a marked decrease in water content which was made up during the night. This periodie

² Cairo Sci. Jour., vol. 5, p. 221, 1911.

³ Trans. Royal Soc. Can., ser. 3, vol. 10, p. 55, 1916, see also Bull. Torr. Bot. Club, vol. 40, p. 1-26, Jan., 1913.

⁴ Bot. Gaz. vol. 53, p. 319, April, 1912.

diurnal condition of dessication has been found by Livingston and Brown to serve as a check on the absolute transpiration and has been termed "incipient drying." Lloyd⁵ independently obtained similar results in his investigations on *Fouquieria splendens* and Mrs. Shreve⁶ established the same phenomenon in 1913 with *Parkinsonia microphylla*.

Inasmuch as the genus *Citrus* is undoubtedly a mesophyte of tropical origin and therefore grown in the interior valleys of California under purely artificial conditions,⁷ it would naturally be expected that the abnormal water relations above discussed might obtain to an unusual degree, especially during the hot growing period, when the ability of the plant to make up for excessive transpiration is taxed to the limit. Citrus fruits are borne on wood of the current season's growth which ordinarily bears six to eight leaves on the same fruiting shoot. Therefore, it seemed reasonable that under conditions of excessive transpiration the leaves might draw on the water supply of the fruits and thus bring about an abnormal water relation. With the above considerations in mind it occurred to the writer that this premature fall of the fruits might be due to irregularities or abnormalities in the water relations between the fruits and foliage, resulting in abscission in some way analogous to the shedding of cotton bolls under the stimulus of a water deficit.

The method used in obtaining the data here presented consisted in the main of simple moisture determinations of leaves and fruits of various kinds taken at different hours of the day. The material was gathered and quickly placed in weighing cups fitted with ground glass covers. After weighing, the material was thoroughly dried and then reweighed. For convenience in the case of fruits and large leaves, the material was cut into small pieces. The calculations are based on the dry weight of the material, except as otherwise stated. The data obtained are shown in condensed form in table 1. The figures shown represent averages of at least ten duplicate determinations, and in most instances of more.

The data presented in table 1 show some very interesting conditions. It is quite clear that, with the exception of the new succulent growth, the young fruits are at all times higher in water content than the leaves situated near them. These data also seem to leave no doubt

⁵ Plant World, vol. 15, p. 11, 1912.

⁶ Ann. Rpt. Dir. Bot. Res. C. I. W., Feb. 12, 1913, p. 81.

⁷ For a more complete discussion see Livingston, B. E., "A single index to represent both moisture and temperature conditions as related to plants," *Physiological Researches*, vol. I, No. 9, April, 1916.

TABLE 1
AVERAGE MOISTURE CONTENT

Kind of material	Average water content in per cent (Dry weight)
New leaves about two weeks old	242.0
Full grown leaves of current season's growth	162.2
Leaves of one season's growth—about one year old	132.7
Leaves of two season's growth—about two years old	126.1
Leaves of three or more season's growth. Over two years old	117.6
Leaves of current season's growth. Gathered between 9 A.M. and 12 P.M.	164.9
Same gathered between 1 P.M. and 4 P.M.	157.2
Leaves of current season's growth gathered from behind fruits between 9 A.M. and 12 M.	166.8
Same gathered between 1 P.M. and 4 P.M.	160.4
Fruits destined to subsequent abscission, one-third to three- fourths inch in diameter	191.5
Fruits apparently normal gathered between 9 A.M. and 12 M. ⁸	260.2
Same gathered between 1 P.M. and 4 P.M.	247.7
Fruits destined to subsequent abscission gathered between 9 A.M. and 12 M.	201.4
Same gathered between 1 P.M. and 4 P.M.	179.2

of the fact that as the leaves grow older there is a progressive decrease in water content.

It is also quite evident that a regular diurnal decrease in the water content of leaves of the current season's growth is manifest during the afternoon. Such leaves averaged 164.9% in water content for the period between 9 A.M. and 12 M. and only 157.2% for the period between 1 P.M. and 4 P.M. This difference does not appear significant when viewed in the light of the large differences obtained by Livingston and Brown with some of their material. However, it should be borne in mind that those authors were dealing, for the most part, with much more succulent plants containing a large amount of water storage tissue. Further, it should be noted that these figures are averages, since the determinations on which they are based were not made at the same hours. Individual pairs of determinations frequently showed differences of as much as 25% to 30% in as short a period as six hours. On June 5 at 2:30 P.M., with the temperature at 95° F and the relative humidity at 19%, the water content of leaves of the current season's growth was 144.3%. At 4 A.M. the next morn-

⁸ The fruits used for these determinations averaged a little larger than those gathered in the forenoon and therefore would normally be somewhat higher in water content.

ing, with the temperature at 62° F. and the humidity 54%, the water content of similar leaves was found to be 172.6%, showing a difference of 28.3%. This phenomenon is taken to indicate the presence of incipient drying in citrus and is in full accord with the results of the writers above mentioned as well as with those obtained by Lloyd.

Since the young fruits have a higher water content than adjoining leaves which, in turn, exhibit a diurnal decrease in relative water content, the conclusion, *a priori*, that the leaves might possibly draw on the water supply of the fruit during periods of excessive transpiration seemed entirely plausible. If such is the case it would seem that leaves so favorably situated should not show this daily variation, at least to the degree shown in the leaves not so favorably situated. The data in table 1 show, however, that the average difference in water content of the two sorts of leaves gathered in the forenoon and afternoon is quite small. This is taken to indicate that if such leaves do utilize the water supply of the fruits, the evaporating power of the atmosphere is so strong that as fast as they receive this surplus water, it is lost and thus causes no appreciable difference in their relative water content.

The next step was to ascertain the water content of different kinds of fruits, those destined to remain and mature, and those showing indications of subsequent abscission. It is quite easy to distinguish between the two, from a week to ten days before abscission occurs, by the difference in their appearance. Exposed fruits destined to drop exhibit a small yellow spot about the navel end several weeks before the actual drop occurs. This spot gradually extends and spreads until at abscission it usually occupies at least half the area of the fruit. In the case of well-shaded fruits, the yellow color is evenly distributed over the entire surface. A large number of moisture determinations were made which showed that those fruits destined to subsequent abscission averaged 59% less water than those fruits destined to remain and mature. (See table 1.) The presence of this condition in the fruits, especially when considered in connection with the daily increase at certain hours in the water deficit of the leaves immediately behind them, seems to point to the possibility of the leaves depriving the fruit of a part of their normal water supply. It certainly indicates an abnormal water relation.

Lemon growers prune their trees at all seasons of the year, even while the fruit is still on the trees. It is a well established practice to gather the good fruit from the excised branches immediately, in order to prevent it from becoming flaccid. Inasmuch as the fruit, as ordi-

narily picked from the tree, remains turgid for several months, it is the common belief that the leaves draw the water out of the fruit when the branch is severed from the tree. That this is exactly what does occur, when the leaves are deprived of their normal water supply, is shown by the following experiments:

Experiment 1—Two shoots bearing small terminal oranges of approximately the same size and having the same number of leaves and approximately the same leaf area, were taken to the laboratory, placed on the table and allowed to dry under similar conditions except that in one case the fruit was severed from the stem. All cut surfaces were sealed with vaseline.

Within twelve hours a marked difference in appearance was observed. The leaves on the shoot from which the orange was detached were considerably shriveled while those on the other shoot remained turgid and fresh. This difference became more pronounced as time elapsed and in thirty hours a distinct difference in the appearance of the fruits as well as leaves was visible. The detached fruit remained firm and retained its dark green color and lustre while the attached fruit was soft and flaccid and exhibited a dull green color without lustre. This experiment was performed repeatedly with both oranges and lemons with the same results. (See plate 12, fig. 1.)

As all the cut surfaces were sealed, it seems clear that the leaves on the shoot with fruit attached actually drew on its water content and that it was this supply of water which enabled them to remain alive and fresh long after the leaves on the other shoot had withered and died.

Experiment 2—Quantitative data on water content were desired to substantiate the visible indications described in Experiment 1. Therefore the latter was repeated several times and moisture determinations on leaves and fruits were made at various periods. A representative set of such determinations is given in table 2:

TABLE 2
MOISTURE CONTENT DETERMINATIONS, TWENTY-FOUR HOURS AFTER BEGINNING
OF EXPERIMENT 2

Kind of material	Weight of container and fresh material in grams	Weight of same when dry	Weight of material in grams	Water content per cent
Orange detached from branch.....	23.40	21.670	2.665	185.0
Orange attached to branch.....	23.585	22.367	2.075	142.1
Leaves from branch with fruit removed	{ 21.831 22.045	21.805 22.010	.181 .170 21.4 avg.
Leaves from branch with fruit attached	{ 21.345 20.604	21.275 20.477	.175 .284 73.7 avg.

These data show that after twenty-four hours the leaves on the shoot with orange attached contained an average of 52.3% more water than those on the other shoot. They further show that the detached fruit contained 42.9% more water than the attached fruit from which the leaves had been drawing their supply. This is considered to be conclusive evidence that in the case of excised branches the leaves can draw water from the fruit.

Experiment 3—Two shoots in every respect similar to those used in the previous experiments were treated in the same manner as those of Experiment 1 and 2. These were then weighed at irregular intervals until they had reached a constant weight. During the interim they were kept on the laboratory table. The data obtained are found summarized in table 3:

TABLE 3
WATER CONTENT DETERMINATIONS MADE AT IRREGULAR INTERVALS BASED ON
THE WHOLE WEIGHT

Number of hours elapsed	Shoot with orange attached				Shoot with orange detached			
	Weight in grams	Loss in grams	Loss in per cent	Difference in per cent	Weight in grams	Loss in grams	Loss in per cent	Difference in per cent
0	4.872	4.777
3	4.436	.436	8.9	.6	4.380	.397	8.3
19	3.957	.915	18.7	3.830	.947	19.8	1.1
21	3.895	.977	20.0	3.742	1.035	21.7	1.7
24	3.803	1.069	21.9	3.607	1.170	24.4	2.5
26	3.683	1.189	24.4	3.442	1.335	27.9	3.5
27	3.610	1.262	25.9	3.342	1.435	30.0	4.1
44	3.263	1.609	33.0	2.911	1.866	39.1	6.0
49	3.047	1.825	37.4	2.682	2.095	34.8	6.4
51	2.920	1.952	40.0	2.575	2.202	36.0	6.0
91	2.125	2.747	56.3	2.008	2.769	57.9	1.6
96	2.053	2.819	57.8	1.960	2.817	58.9	1.1
99	2.000	2.872	58.9	1.935	2.842	59.5	.6
116	1.921	2.951	60.5	1.873	2.904	60.8	.3
119	1.894	2.978	61.1	1.852	2.925	61.2	.1
121	1.881	2.991	61.3	1.844	2.933	61.4	.1
140	1.825	3.041	62.5	.4	1.807	2.970	62.1
146	1.797	3.075	63.1	.5	1.783	2.994	62.6
162	1.774	3.098	63.5	.6	1.770	3.007	62.9
186	1.736	3.136	64.3	.8	1.743	3.034	63.5
195	1.717	3.155	64.7	.9	1.726	3.051	63.8
211	1.705	3.167	65.0	1.1	1.720	3.057	63.9
218	1.695	3.177	65.2	1.0	1.710	3.067	64.2
260	1.666	3.206	65.8	1.1	1.686	3.091	64.7
285	1.652	3.220	66.0	1.1	1.675	3.102	64.9
306	1.642	3.230	66.2	1.1	1.664	3.113	65.1
330	1.631	3.241	66.5	1.1	1.652	3.125	65.4
525	1.613	3.259	66.8	1.0	1.631	3.146	65.8

The data in this table indicate that the amount of water in the fruit available for use by the leaves was sufficient to maintain the latter alive for approximately 50 hours after the shoot was cut from the tree. It is further evident that when three hours had passed the leaves on the shoot with fruit attached had not yet begun to take water from the fruit to any appreciable extent because the shoot with fruit detached shows less water loss than the shoot with fruit attached. However, this condition was soon reversed and the leaves began to

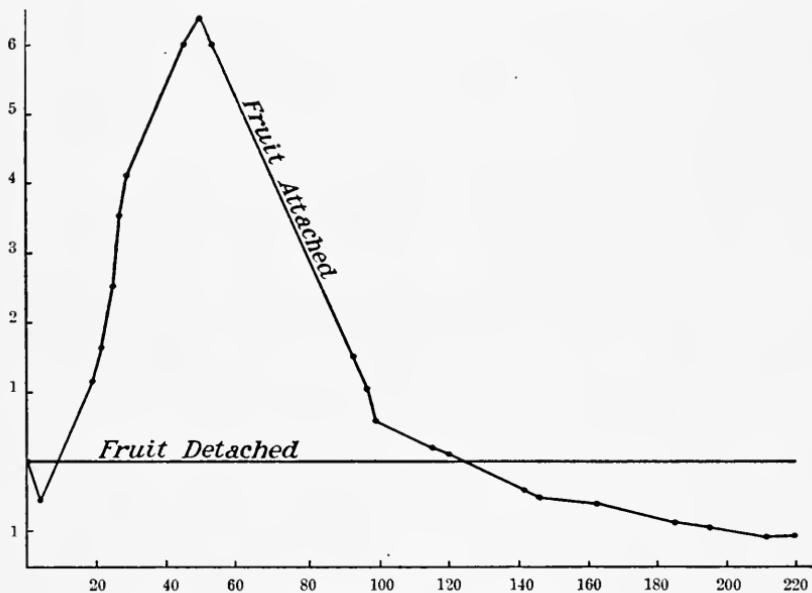


Fig. 1. Showing the difference in per cent of water loss of shoot with orange attached and shoot with orange detached. The water loss curve of the shoot with fruit detached is considered as normal. Ordinates represent differences in per cent of water loss, abscissae, the time elapsed in hours. Water content calculated on basis of fresh weight.

draw on the water in the fruit while the leaves to which no water was available from the fruit showed indications of wilting.

That shortly after 50 hours had passed death occurred in the leaves of the shoot with fruit attached is shown by the rapid increase in the amount of water loss. This was undoubtedly due to increased permeability of the cytoplasmic cell membranes after death. After 50 hours the difference in water content of the two was 18.3% in favor of the shoot with fruit attached. However, from this time on until both had reached a constant rate of water loss (after about 200

hours), this shoot lost water more rapidly than the shoot with fruit detached. These relations are very clearly shown in figure 1. The normal water loss curve is illustrated in figure 2.

Experiment 4—A forked twig bearing a small terminal fruit on each branch was selected and cut. The fruits were immediately immersed in water and the shoot tied to a support in such a fashion that all the leaves were exposed to the air, the fruits alone being immersed. One orange was now removed by cutting it under water and all cut surfaces were sealed. The two fruits remained under

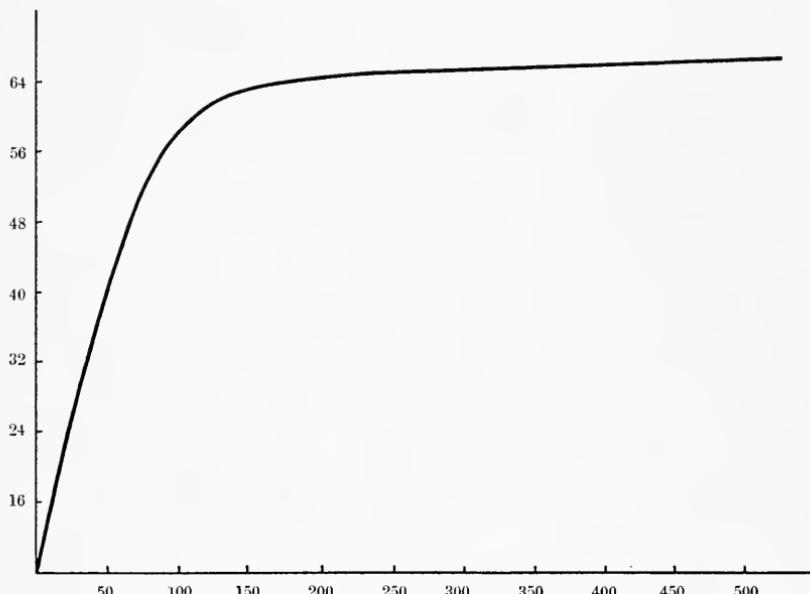


Fig. 2. Showing the general type of water loss curve of a shoot detached from the tree, including detached orange. Ordinates represent water loss in per cent and abscissae, the time elapsed in hours.

water. The container and support were then placed on a bench in the shade in the open air and left for fifteen hours, at the end of which time moisture determinations were made on the fruits.

TABLE 4
MOISTURE DETERMINATIONS AFTER FIFTEEN HOURS

Kind of material	Weight of container and fresh material in grams	Weight of same when dry in grams	Weight of material in grams	Water content per cent
Detached orange	24.680	21.435	3.330	206.9
Attached orange	23.210	21.773	2.570	126.8

The data in table 4 show that at the end of fifteen hours there was a difference in water content between the two fruits of 80.1%. There seems to be no way of accounting for this large difference other than that the leaves had actually drawn the major part of it at least, from the attached fruit.

WATER TRANSPORT STUDIES BY MEANS OF DYE STUFF SOLUTIONS

Experiment 5—Bearing the foregoing findings in mind, it seemed desirable to determine something of the nature of this reversal of normal water flow by means of dye solutions. Accordingly a shoot bearing a terminal fruit was cut from the tree and the orange pared away at the apical end to open the tracheal elements and admit the dye.⁹ This paring was done under the solution to prevent the entrance of air bubbles. Water soluble eosin was used. The orange was immersed in the liquid for a half hour, after which the shoot was split open. The tracheal tubes throughout all parts of the leaves, stems and fruits were found to be strongly stained.

Experiment 6—It seemed desirable to simulate the actual situation on the tree as nearly as possible and the following experiment was designed to accomplish this. A crooked fruiting branch bearing a number of small lateral shoots and leaves, and one terminal orange was cut under water. The cut end was kept under water and the branch so supported that the fruit was immersed in an eosin solution. The apex of the orange was then pared as described above. The branch then rested with its basal end in water and the vascular bundles of the fruit open to eosin at the other end of the branch. (See pl. 12, fig. 2.) If we substitute for the water container the conducting system of the tree, and for the watery solution of eosin the developing fruit high in water content, we have very similar conditions to those existing in the experiment, save for the fact that the fruit is not open to the air and the conducting system bears a certain relation to the rest of the tree.

The experiment was begun late in the afternoon and the branch left outdoors over night. At 8 o'clock the next morning the leaves were examined and found to be very fresh and turgid. Indeed they were noticeably much fresher in appearance than they had been the evening before. On careful examination absolutely no trace of eosin

⁹ It should be stated here that the Washington Navel orange is in reality a double fruit, with a small secondary orange within a large primary fruit. This interior fruit constitutes what is known as the navel and it possesses an independent vascular system of its own which traverses the central pith of the primary fruit before ramifying through the secondary orange. This central pith thus acts as the stem to the small fruit.

could be found in any part of the shoot. Samples of leaves for moisture content determination were taken at 8:30 A.M. Although remaining in the shade the leaves showed at 12:15 P.M. distinct evidence of wilting and upon examination, eosin staining was found in the petioles of every leaf on the shoot, with the exception of a few on the extremities of the side branches. At 12:30 P.M. samples were taken for moisture determination.

TABLE 5
MOISTURE CONTENT OF LEAVES TO WHICH WATER WAS AVAILABLE FROM
TWO SOURCES

Hour picked	Weight of container and material in grams	Weight of same when dry in grams	Weight of material in grams	Average water content in per cent
8:30 A.M.	21.967	21.617	.562
	23.455	23.162	.480	160.8
12:30 P.M.	21.914	21.659	.459
	21.552	21.345	.382	121.6

The data obtained in this experiment show that during the night, when the draught of the atmosphere on the water supply was low, the leaves were able to maintain themselves in a normal condition by using water from the base container. This is evidenced by the normal water content of the leaves in the morning, as well as indicated by the fact that no eosin whatever was drawn back, although the vascular bundles were open to its entrance. However, as the atmospheric evaporating power increased during the forenoon, it became more and more difficult for the leaves to obtain requisite amounts of water through the conducting system in the normal way. At a point near 12 M. the leaves became unable to obtain enough water in this fashion and they began to draw on the aqueous solution of eosin. The shoot was now drawing water from both ends to satisfy the demands of the transpiring leaves. But the atmospheric pull for water became so severe that even this double supply did not suffice to maintain the water content of the leaves at normal. The water deficit began to increase and continued until a condition of actual wilting resulted. Between 8:30 A.M. and 12:30 P.M. the leaves decreased in water content by 39.2%, although both ends of the shoot were immersed in water.

From the evidence above presented it seems clear that under conditions favorable to rapid transpiration it is entirely possible for the leaves of citrus trees, at least, to draw water back from the young fruits. Moisture determinations of fruits under such conditions showed a considerable decrease in water content and indicated that

this water is utilized by the leaves. Indeed, almost exact quantitative results were obtained, the percentage of water loss of the fruit being approximately equal to that gained by the leaves. (See Experiment 2.) Dye stuff experiments have shown that there exist no physical difficulties for such procedure. It then remained to determine whether this phenomenon actually occurred in fruits on the tree. For this purpose the procedure of the previous experiments was used, namely, moisture determinations and water transport studies by means of dye stuff solutions. However, the evidence here is not so conclusive, as all the experimental work was necessarily performed on shoots *in situ*, which introduces a number of uncontrollable adventitious variables, as has been well pointed out by Dixon¹⁰ in his criticism of transpiration measurements performed on shoots detached from the tree. The influence of the remainder of the tree is admittedly an unknown quantity. Nevertheless it is believed that the data obtained are strongly indicative of conditions as they exist.

From table 1 it will be seen that there exists a considerable difference in water content between those fruits, destined to remain and mature when picked before and after noon. Fruits of this sort gathered in the morning averaged 12.5% more water than those gathered in the afternoon. As is mentioned in the footnote to table 1 this difference is probably considerably smaller than it should be on account of the larger size of the fruits used in the afternoon determinations. That this same condition obtains in those fruits destined to subsequent abscission is also shown in table 1. In this case the difference is 22.2%. There are several ways in which a decrease of water content in the fruit can be explained: (1) the water is actually drawn back from the fruits by the leaves; (2) the normal supply to the fruits is considerably reduced by being appropriated by the leaves before it reaches the fruits; or (3) the transpiration ratio of the fruit to the leaves is markedly increased. If the fruit possessed no stomata and did not transpire, the first condition must hold. However, the fruit does possess stomata in some numbers and is actively transpiring at the same time as the leaves. Therefore it seemed advisable to make a cursory comparative study of the number of stomata per unit of area on the fruits and leaves and also of the ratio of transpiring area of the fruits and leaves situated immediately behind them. While the young fruit possesses stomata even before the style is exfoliated, stomatal counts showed that the number is comparatively small, rang-

¹⁰ Transpiration and the ascent of sap in plants (London, MacMillan, 1914), pp. 120-125

ing between 50-100 per square millimeter as compared to 300-450 per square millimeter on the leaves. Measurements of the leaves situated within six inches of the fruit showed that, in addition the leaf area immediately behind the young growing fruit is larger than the area of the fruit until it reaches approximately two inches in diameter, after which falling of the fruit is comparatively rare. Therefore, it seems highly probable that the transpiration of the fruit as compared to that of the leaves situated immediately behind it is an almost negligible factor and it appears reasonably certain that either water is actually drawn back or that the normal supply is decreased.

Considering these two possibilities, the first merits more consideration as it is supported by proof which, though not absolute, is at least presumptive evidence of a strong enough character; while on the other hand the second possibility, agreeing though it does with the most recent theory on sap movements in plants as put forth by Dixon, is still a theoretical consideration. According to this theory, which postulates strong tensions existing in the ascending water columns, no assumption of an actual reversal of the current is necessary in order to explain a decrease in moisture content. During normal conditions the relation between the tensions existing in the water columns leading to the fruits and those leading to the leaves is such that both organs receive an adequate water supply. The tension existing in any one of these water columns is a function of the transpiring force existing in the transpiring plant organ as modified by atmospheric conditions. Therefore, as these transpiring forces vary, the tensions vary. Transpiration from the leaves, for reasons pointed out above, is subject to much greater variation than that from the fruits. Therefore during periods when evaporation is greatly accelerated the tensions in those water columns leading to the leaves are greatly increased and as a consequence more water is drawn to them. As the source of supply in the conducting system is practically constant, the amount in the fruits is thereby reduced and this results in a decrease of relative water content of a magnitude conditioned by the transpiration of the fruit.

However, it should be noted that the data in table 1 show a decrease in absolute water content of the fruit of 15% to 20%, a loss of considerable magnitude. There are only two ways in which such a decrease in absolute water content can take place: (1) the water is lost by transpiration from the fruit, or (2) it is drawn back by the leaves. But since the fruit possesses a very small stomatal area

as compared with the leaves and, moreover, it is highly probable that a large percentage of this area is non-functional, being obstructed by accumulations of a resinous nature, there is small likelihood for absolute loss of water in this manner to the extent noted. Hence there seems but one way to explain it and that is by movement back from the fruits.

Evidence of an indirect nature pointing to the same conclusion lies in the fact that there are some indications that abscission of a certain proportion of the young fruits is directly due to the influence of hydrolysing enzymes secreted by certain saprophytic or facultative parasitic fungi always found present on the shriveled style* and frequently in the proliferations of the navel. Such enzymes in order to act on the abscission layer must be drawn back through the vascular systems of the fruit into the pedicel where this layer is located. Investigations on this point are now in progress.

Experiment 7—Three similar fruits were selected on different parts of a tree; on one of the lower branches in the shade, at a height of four feet, and in the top of the tree in full sunlight. At noon each fruit was pared so as to admit entrance of a solution and then plunged quickly into a small vial containing a watery solution of eosin. These vials were securely tied to the shoot and left suspended for two hours. At the end of that time, on cutting leaves from these shoots, eosin staining was found in the vascular systems of all. On examining backward toward the tree, eosin was found as far back as thirty centimeters. This experiment was repeated a number of times both at Edison and at Riverside and uniformly gave the same results, although much less marked at the latter place. In every case the backward movement of the eosin solution was at its maximum during the afternoon.

Cutting the ends of branches *in situ* under a watery solution of eosin was tried at different times of day and gave similar results. This experiment was performed at Edison, Riverside and Indio. At the latter place, with the temperature at 116° F and the humidity at 8% the eosin solution traveled backward at the astonishing rate of 30 cm. per minute at 6 P.M. Similar results were obtained using *Eucalyptus rufa* as material. In fact with long slender poles of *Eucalyptus tereticornis* at Edison, such a remarkably rapid backward flow of eosin was observed (105 cm. in one minute) in the afternoon as to compel the conclusion that after all, the force responsible for this movement under such conditions must be negative pressure pro-

duced by rapid transpiration rather than a mere difference in osmotic concentration of the solutions involved. Moreover, negative pressure produced by transpiration would seem a more plausible explanation of the results obtained by Chandler¹¹ with tomato plants and by him attributed to osmosis. For as Dixon¹² has pointed out "it is quite possible for the solvent, water, to be in a state of tension, i.e., at a negative pressure, while the dissolved substance may be at a positive pressure and be active as a distending force in the cell."

These experiments, it is believed show that, during the afternoon at least, strong negative pressures exist in the water columns of citrus trees under the climatic conditions here considered and that the young developing fruits are deprived periodically of a part of their water supply by excessive transpiration from the leaves.

During the June-drop period of 1916 a number of holes were dug in various parts of the Edison orchard to a depth of six feet and moisture determinations made at various depths and on all sides of the tree. The moisture content was found to range between 5%-6% just before irrigation and between 10%-12% soon after irrigation. A fruit grower observing this soil and the vigorous growth of the trees would hardly conclude that the trees were suffering from lack of water. However, the specific effect of variations in the moisture content of the soil on the transpiration rate and water content of orange leaves has not yet been carefully determined. While there is little room to doubt that the above-ground complex is more important in influencing transpiration than the below-ground complex, still it is entirely possible that this abnormal water deficit in the leaves and fruit may be more easily induced by sudden changes in the climatic complex under conditions of a deficient moisture supply in the soil or, what amounts to the same thing, an inhibition of the normal absorption due to lack of sufficient aeration or excessively high soil temperatures. Nevertheless evidence is not lacking that marked changes in air temperature and humidity may be sufficient to cause abscission of young fruits even though the soil moisture conditions be ideal. Such apparently is the explanation of the heavy drop of Washington Navels already referred to, which occurred over most of the citrus districts immediately following the excessive temperatures of June 15-17, 1917, when the mercury reached 110-120° F in many parts of the citrus district south of the Tehachapi mountains.

¹¹ Mo. Sta. Res. Bull. 14, pl. 13.

¹² *Loe. cit.* p. 140.

CONCLUSION

This paper deals with one phase of an investigation of a so-called physiological disease, June drop of the Washington Navel orange. An excessive dropping of the young fruits has been experienced for years in the dry interior valleys of California and Arizona.

An abnormal water relation is found to obtain periodically in citrus foliage and in the young fruits during the hot growing season in these regions. A diurnal decrease in water content of the fruits occurs during the afternoon and is accompanied by a considerable increase in the water deficit of the leaves. Negative pressures of considerable magnitude are found in the water columns of citrus trees under these climatic conditions. These attain their maximum during the afternoon. The dropping of the fruits appears to be most severe where the above mentioned water relations are most abnormal.

Inasmuch as in the case of certain other plants the abscission of young fruits has been shown to be due to abnormal water relations it is suggested that such may be the case here.

In conclusion, the writer wishes to acknowledge his indebtedness to Professor J. Eliot Coit, under whose supervision and with whose assistance a large part of the experimental work was done; also his obligations to Professor Charles B. Lipman for his kindly interest in the investigation and for his many useful suggestions, and to the Edison Land and Water Company for their kind and courteous coöperation.

PLATE 12

Fig. 1. Showing extent to which the leaves can draw on the water in the fruit. Both shoots were cut at the same time and had approximately the same leaf area. All cuts were sealed with vaseline. The fresh-appearing leaves on the shoot at the left have maintained themselves at the expense of water in the fruit. Note the difference in reflection of light from the two fruits. See Experiment 1.

Fig. 2. Photograph illustrating an orange shoot so arranged as to be able to draw water from one end and eosin solution through the pared apex of a small fruit at the other. In spite of this double supply a large water deficit occurred, and eosin was drawn back from the container on the right to the leaf next to the water container on the left. See Experiment 6.



Fig. 1



Fig. 2

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